PREDATION OF ARTIFICIAL SAGE GROUSE NESTS IN TREATED AND UNTREATED SAGEBRUSH

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ABSTRACT.—We measured predation on 120 artificial Sage Grouse (Centrarcus urophasianus) nests in montane sagebrush grassland in northern Utah. We examined nests in areas that had been chained and seeded 25 years previously (treated areas) and in areas that were untreated. Predation rates of artificial nests were higher in areas of untreated sagebrush, even though these areas had greater sagebrush cover, taller shrubs, and greater horizontal plant cover. These results differ from those previously hypothesized for treated sagebrush habitat and may reflect a greater abundance of other potential prey species, especially lagomorphs, in untreated areas that attracted greater densities of predators. In addition, over 80% of nests were depredated by mammals, which hunt using olfaction and are less likely than avian predators to be affected by nest cover. We conclude that, after treated sagebrush has recovered to some degree, predation rates of Sage Grouse nests may be lower in treated sagebrush. Consequently, factors other than nest predation (e.g., winter food, thermal cover, insects, perennial forb abundance) may be more important reasons for preserving mature sagebrush stands for Sage Grouse.

Key words: Sage Grouse, Centrarcus urophasianus, sagebrush, nest, predation, habitat.

A key problem in the conservation of wildlife species is fragmentation of large contiguous areas of preferred habitat (Lovejoy et al. 1984, Wilcove 1985, Yahner and Scott 1988), a problem that has plagued the management of upland game bird populations in western North America (Vale 1974, Braun et al. 1977). In particular, Sage Grouse populations have declined in some areas, apparently in response to widespread treatment (chaining, spraying, burning, etc.) of sagebrushdominated rangeland to benefit livestock production (Schneegas 1967, Klebenow 1970, Braun et al. 1977). However, few studies have examined whether such treated areas can recover to become suitable Sage Grouse habitat.

Sagebrush treatment may reduce Sage Grouse populations by eliminating mature shrubs, which may be important in protecting nests from visual predators (Dalke et al. 1963, Braun et al. 1977, Autenrieth 1981, Connelly et al. 1991). In addition, treated areas planted to grass cover (e.g., crested wheatgrass, Agropyron desertorum) often recover shrubs slowly (Vale 1974, MacMahon 1987). Sagebrush treatment may therefore permanently reduce nesting cover.

For ground-nesting birds in general, dense shrub cover may not always be beneficial; it may increase nest predation by supporting greater populations of alternate prey and attracting greater densities or attention of predators (Croze 1970, Duebbert and Kantrud 1974, Taylor 1977, 1984). Alternate prey, however, may sometimes decrease nest predation by diverting predator effort during nest incubation (Byers 1974, Weller 1979, Crabtree and Wolfe 1988). For areas recovering from sagebrush treatment that have relatively low shrub cover, it is not clear whether Sage Grouse nest predation is greater than in untreated areas with greater cover.

In this study we tested the hypothesis that artificial Sage Grouse suffer higher predation rates in treated than in untreated sagebrush. We also measured vegetation characteristics associated with nest sites to determine which habitat components might contribute to nest predation. Finally, we measured indices of lagomorph, small mammal, and predator abundance within treated and untreated areas to establish whether higher nest predation rates were associated with a higher density of alternate prey and/or predators.

STUDY AREA

The study was conducted on the property of Deseret Land and Livestock, an 80,000-ha ranch located in northwestern Utah along the

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Wyoming border (Rich County). We conducted the study on mid-elevation (2000 m) benches dominated by Wyoming big sagebrush (Artemisia tridentata wyomingensis), rabbitbrush (Chrysothamnas viscidiflorus), and several herbaceous species, mainly western wheatgrass (Pascopyrum smithii), needleand-thread (Stipa comata), Indian ricegrass (Oryzopsis hymenoides), bluegrass (Poa sandbergi), and Phlox spp.

Many separate 1000-5000-ha pastures, totalling nearly 40% of the 32,000 ha of midelevation sagebrush grassland on the ranch, were treated by discing or spraying between 1960 and 1965, resulting in a partial loss of sagebrush. These treated areas were seeded with crested wheatgrass (Agropyron desertorum) to improve forage for livestock. Thus, two distinct habitats exist on the study area: untreated areas with 5-20% herbaceous cover and 10-40% shrub cover (mostly sagebrush), and treated areas with 5-40% herbaceous cover (mostly crested wheatgrass) and 0-20% shrub cover (mostly sagebrush and rabbitbrush). Treated areas typically had recovered some shrub cover, but shrubs were shorter and less dense than in untreated areas.

Alternate prey for potential Sage Grouse nest predators included lagomorphs (whitetailed jackrabbits [Lepus townsendi], mountain cottontails [Sylvilagus nuttalli], and pygmy rabbits [Brachylagus idahoensis]) and small mammals (Peromyscus maniculatus and Perognathus parvus). The primary mammalian nest predators were covotes (Canis latrans), badgers (*Taxidea taxus*), and chipmunks (Eutamias minimus). Principal avian nest predators were Common Ravens (Corvus corax), Black-billed Magpies (Pica pica), and California Gulls (Larus californicus) (all Sage Grouse leks [breeding grounds] in the study area were within 10 km of a large gull colony on Neponset Reservoir).

METHODS

Artificial Nests

Predation rates of artificial nests were measured in each habitat type during the Sage Grouse nesting season of 1991. We set up artificial nests at 160-m intervals along three 1.6-km transects radiating at random compass bearings and commencing 0.8 km from each of four Sage Grouse leks (two in each habitat

type). These locations represented the area most likely used for nesting by females attending each lek (Wallestad and Pyrah 1974, Beck 1977). Thus, we used a total of 120 nests, with 10 nests per transect, 3 transects per lek, and 2 leks per habitat type. To achieve some level of replication, we selected 2 leks in each habitat type so that sampling areas delineated by a 2.2-km radius surrounding each lek did not overlap and included different groups of pastures. Leks in treated areas were located in pasture complexes treated in different years and separated by untreated sagebrush.

We drove along each transect in a vehicle to avoid leaving a scent trail. At each 160-m interval, we placed artificial nests under the closest shrub (>10 cm height) to a point at a random distance (10–30 m) along a line perpendicular (randomly left or right) to the main transect. These precautions were taken to reduce the chance that avian predators could "cue" on artifical nests by following tire marks along the main transect (Galbraith 1987, MacIvor et al. 1990) and the chance that mammalian predators could detect nests by following human scent. However, either type of predator could have followed tracks left by the vehicle.

Each "nest" consisted of three unmarked brown chicken eggs. Nests were placed in the field between 30 April and 3 May 1991 during the Sage Grouse nesting period at Deseret Ranch. Nests were checked 15 days later and were considered depredated if all eggs were destroyed or missing, or partially depredated if one or two eggs remained. We attempted to identify the nest predator as either mammalian or avian, based on characteristics of egg remains (Rearden 1951, Patterson 1952). We could identify likely predators at 43 of 57 depredated nests.

Habitat Characteristics

We measured vegetation characteristics, alternate prey abundance, and badger abundance at or near artificial nest transects to evaluate potential differences among habitat types. We measured vegetation characteristics when artificial nests were checked for predation. Specifically, we estimated percent cover of shrubs and herbaceous plants as well as height of the tallest shrub in four Daubenmire (1968) plots at each nest site. These plots were spaced 5 m apart along a 20-m transect

extending from the nest site and parallel to the main artificial nest transect. We measured horizontal cover by counting the number of 5 × 5-cm squares on a 45 × 45-cm board that were obscured by the nest bush to a viewer at 10 m distance and 40 cm height (Jones 1968, Klott and Lindzey 1990).

Abundance of alternate prey for potential predators was estimated in July 1991 in both sagebrush habitat types within 1 km of the artificial nest transects. We estimated lagomorph abundance by counting the number of lagomorph fecal pellets in ten 2 × 2-m plots located every 15 m along 150-m transects. We counted fecal pellets along four randomly located transects in each habitat type. We estimated abundance of small mammals by establishing two replicate 200 × 200-m grids of 25 Sherman[®] live traps placed 50 m apart in each habitat type. Traps were baited with rolled oats and peanut butter and checked for 3 nights (11–13 July).

We estimated abundance of badgers, a principal mammalian nest predator, by counting the number of active badger holes seen along 2.5-km transects in mid-July 1991. Nine transects were randomly located within 1 km of artificial nest sites in each habitat type. Active badger holes were identified by fresh digging, a large oval hole, and presence of scat and/or tracks.

Statistical Tests

Proportions of nests depredated were compared with chi-square tests for treated vs. untreated areas and with Fisher's Exact Test for mammalian vs. avian predators. We compared the mean proportion of depredated nests and vegetation characteristics in treated vs. untreated areas with a nested ANOVA (Dowdy and Wearden 1991) with leks as experimental units and transects as subsamples. All proportions were arcsine-square root transformed for statistical tests to equalize variance of proportions (Neter and Wasserman 1974). Because there were only two replicate leks in each habitat type, the design had a low power to detect differences (Neter and Wasserman 1974). Consequently, we selected an alpha of .10 for significance tests in the nested ANOVA.

We compared the abundance of lagomorphs, small mammals, and badgers between habitat types using t tests. Each walked transect was considered a subsample of badger abundance within each habitat type. The relationship between different vegetation characteristics and nest success was analyzed for two sampling units, transect and nest, that measured habitat characteristics at different scales. With transects as sampling units, the relationship between mean vegetation characteristics and proportion of nests depredated on each transect was tested using multiple linear regression and partial correlation. With nests as sampling units, the relationship between vegetation characteristics and nest success at individual nest sites was tested with multiple logistic regression. All statistical tests were performed using NCSS (Number Cruncher® Statistical System).

RESULTS

Female grouse attended leks (8–20 males/lek) and nested in both treated and untreated sagebrush. Of 22 hens radio-collared on wintering areas between 1985 and 1989, 9 nested in treated areas the following spring (R. Danvir unpublished data). This frequency (40.9%) was not significantly different from the proportion of sagebrush grassland on the ranch that had been treated (40%) ($X^2 = .009$, df = 1, P > .90).

Overall, artificial nests were depredated significantly less frequently in treated sagebrush (10 of 60) than in untreated sagebrush $(33 \text{ of } 60) (X^2 = 19.5, \text{ df} = 1, P < .001). \text{ Mean}$ proportion of nests depredated was greater in untreated than in treated sagebrush and the difference approached significance (F = 6.3, df = 1,2, P = .12; Table 1). Mean proportion of nests depredated differed significantly among leks (F = 4.6, df = 2,8, P = .04; Table 2). The majority of nests were depredated by mammals (37 of 43), with birds accounting for the remaining 6. The proportion of nests depredated by mammals did not differ significantly among habitat types (treated: 9 of 11; untreated: 28 of 32, Fisher's Exact, P = .63).

Differences in nest predation among habitat types and leks were attributed to differences in vegetation characteristics (Table 1, 2). Horizontal cover (% of cover board obscured) and maximum shrub height were significantly greater in untreated areas, but shrub and herbaceous cover were not (Table 1). Leks varied significantly in horizontal cover, herbaceous cover,

TABLE 1. Artificial nests depredated (%) and habitat characteristics for treated and untreated areas of sagebrush grassland at Deseret Ranch.

Variable	Untreated habitat		Treated habitat				
	\overline{x}	SE	\overline{N}	\overline{x}	SE	\overline{N}	P^{a}
Nests depredated (%)	55.0	16.2	2	16.7	14.3	2	.12
Vegetation characteristics							
Horizontal cover (%)	89.3	2.5	2	69.4	2.4	2	.08
Shrub cover (%)	27.0	1.8	2	17.0	1.7	2	.15
Herbaceons cover (%)	21.1	1.6	2	18.2	1.4	2	.51
Maximum shrub height (cm)	65.0	3.1	2	36.1	2.8	2	.06
Alternate prey abundance							
Lagomorph pellets $(\#/m^2)^{b}$	17.0	3.5	4	2.5	3.6	4	.006
Small mammals (#/100 trap-nights)	8.6	0.8	2	12.6	0.8	2	.02
Predator abundance							
Badger holes (#/km)	2.0	0.52	9	0.67	0.19	9	.02

^aFor nests depredated and vegetation characteristics, nested ANOVA, P < .10 significant, see text; for alternate prey abundance, t tests, P < .05 significant. ^bData were log-transformed to account for nonnormal distributions.

Table 2. Mean proportion of nests depredated and vegetation characteristics (\pm SE, N=3) associated with Sage Grouse leks in treated and untreated sagebrush.

		Lek				
	Untreate	Untreated habitat		Treated habitat		
Variable	Dip	Kate Hollow	Neponset	Alkali Hollow	P^{a}	
Nests depredated (%)	66.7 ± 14.5	43.3 ± 5.8	6.7 ± 6.7	26.6 ± 12.0	.04	
Horizontal cover (%)	89.3 ± 2.2	87.6 ± 5.4	65.3 ± 5.3	75.6 ± 2.8	.09	
Shrub cover (%)	24.3 ± 2.9	29.0 ± 0.7	19.3 ± 3.6	16.0 ± 4.9	.22	
Herbaceous cover (%)	26.0 ± 3.2	17.0 ± 0.7	17.6 ± 0.4	15.7 ± 4.0	.07	
Maximum shrub height (cm)	70.7 ± 3.3	59.9 ± 4.9	33.4 ± 5.6	37.5 ± 5.5	.005	

^aFrom nested ANOVA, P < .10 significant, see text.

and maximum shrub height (Table 2). With transects as sampling units, we regressed proportion of nests depredated along the transect against the transect mean of each of the habitat variables (Fig. 1). Nest predation increased significantly with each variable except shrub cover. Each variable was correlated with each of the others, so we examined the independent effects of each variable by calculating its partial correlation coefficient (Table 3; Neter and Wasserman 1974). Horizontal cover had a significant positive partial correlation with

nest depredation rate, while shrub cover had a significant negative partial correlation. Herbaceous cover showed a positive partial correlation with nest predation that was nearly significant (P=.12), but maximum shrub height showed nearly zero partial correlation with nest predation. Overall, vegetation characteristics measured with transects as sampling units explained 86% of the variation in nest predation.

With nest sites as sampling units, we used logistic regression to analyze the relationship

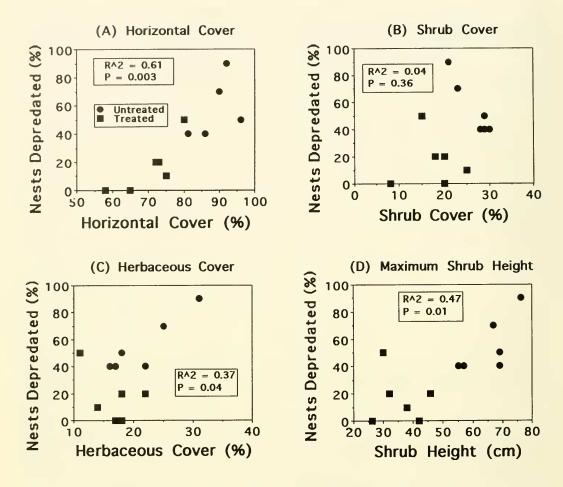


Fig. 1. Relationships of proportion of nests depredated (%) and four vegetation characteristics (see text for precise definitions): (A) horizontal cover, (B) maximum shrub height, (C) shrub cover, and (D) herbaceous cover. R² values are for linear regressions. Data points represent transect means, presented separately for treated areas (●) and untreated areas (■).

between the success (no predation) of individual nests and vegetation characteristics associated with each nest site (Table 4). As was found with transect sampling units, nest predation increased with increasing horizontal cover, herbaceous cover, and maximum shrub height, but not shrub cover. With all four variables considered simultaneously (multiple logistic regression), however, only horizontal cover and maximum shrub height were significant. Overall, vegetation characteristics at nest sites explained only 12% of the variation in nest predation.

Abundance of lagomorphs was significantly greater in untreated areas, but abundance of small mammals (primarily *Peromyscus maniculatus*) was greater on treated areas (Table 1).

Fresh badger holes, however, were significantly more common in untreated areas. Consequently, greater predation of artificial Sage Grouse nests appeared to be associated with higher abundances of lagomorphs and badgers, but lower numbers of small mammals.

Discussion

Predation rates of artificial nests were higher in untreated sagebrush in spite of greater nest cover. These results contrast with those from studies that found greater predation rates on nests in sparser cover (Wallestad and Pyrah 1974, Connelly et al. 1991). However, Autenrieth (1981) found similar results to ours, namely lower predation rates on nests

TABLE 3. Simple and partial correlation coefficients (*N* = 12) of proportion of nests depredated with four vegetation characteristics when all four variables are included in a multiple regression analysis.

Variable	Simple ra	Partial <i>r</i>	P^{b}
Horizontal cover	.78	.89	.0004
Shrub cover	.20	75	.01
Herbaceous cover	.61	.52	.12
Maximum shrub height	.69	04	.90

^aFor P values, see Figure 1.

in a crested wheatgrass planting with sparse (<5%) sagebrush cover than in untreated sagebrush. In addition, Patterson (1952) found higher nest predation rates under taller, denser sagebrush.

At least two patterns emerge that may explain the conflicting results of these studies. First, nest predation was higher when predator densities were higher, regardless of nest cover (Autenrieth 1981, Angelstam 1986, this study). Badgers were the most frequent large mammalian nest predator (Patterson 1952, this study) and were more abundant in untreated areas. Second, nest cover seems to be more important in protecting nests from visually hunting predators, such as ravens, magpies, or gulls (Jones and Hungerford 1972, Picozzi 1975, Autenrieth 1981, Yahner et al. 1989, Sullivan and Dinsmore 1990), than those hunting by olfaction, such as badgers, covotes, or chipmunks. These two patterns suggest that the type and density of predators may affect the degree to which nest cover reduces nest predation (Bowman and Harris 1980, Angelstam 1986).

An additional factor that may explain discrepancies among studies is the fact that our treated areas were >25 years old and had recovered some sagebrush. Wallestad and Pyrah (1974) and Connelly et al. (1991) studied areas that had been recently treated and perhaps still contained pretreatment densities

of predators. In this study predator densities would have had plenty of time to decline following sagebrush treatment. Thus, the effect of habitat on nest predation may be due primarily to the densities of predators supported by the habitat.

Our conclusions are based on artificial nests; several studies have shown that the fate of artificial nests may not reflect that of natural nests (Angelstam 1986, Storaas 1988, Yahner and Voytko 1989). However, fates of artificial nests are likely to reflect differences in predation rates among habitats and are legitimate tools for testing the hypotheses in this paper.

Vegetation characteristics associated with increased nest predation depended on the sampling unit used in the analysis. When transects were used as sampling units, increased nest predation was associated with increased horizontal and herbaceous cover (Fig. 1. Table 3). When individual nest sites were used, horizontal cover and maximum shrub height were the only significant factors (Table 4). Moreover, vegetation characteristics averaged for a transect explained considerably more variance in nest predation (86%) than did characteristics associated with individual nest sites (12%). Thus, the effect of vegetation characteristics on nest predation may depend on the scale at which they are measured (Bowman and Harris 1980, Allen and Starr 1982). In this case, vegetation characteristics of the overall habitat in which nest sites are located (transect scale) may be more important than characteristics directly at nest sites.

The correlation between horizontal and herbaceous cover and increased nest predation at the transect scale may actually reflect an indirect effect of habitat on nest predation rate: greater horizontal and herbaceous plant cover may be preferred by lagomorphs and other small mammals, which may then attract a greater density of predators. A greater density

Table 4. Results of multiple logistic regression of nest predation (0 = nest destroyed, 1 = no predation) vs. vegetation characteristics at individual nest sites.

Variable	Coefficient	SE	Variance explained (%)	P^{a}
Horizontal cover (%)	-0.024	0.012	6.1	.04
Shrub cover (%)	0.010	0.020	0.2	.62
Herbaceous cover (%)	-0.009	0.021	0.2	.65
Maximum shrub height (cm)	-0.021	0.009	6.4	.03

^aFrom x^2 test within multiple logistic regression, P < .05 significant.

 $^{{}^{\}mathrm{b}}P$ value for the partial correlation coefficient

of predators may then inflict a greater predation rate on Sage Grouse nests. Our data are somewhat consistent with this hypothesis, in that lagomorphs and badgers were more abundant in untreated areas, and badger holes were often associated with burrow systems used by cottontails and pygmy rabbits. However, small mammals, which provide a lower prey biomass than lagomorphs, were more abundant in treated areas. Nevertheless, the association between vegetation, alternate prey abundance, predator density, and nest predation rates appears to be the most likely hypothesis explaining our results.

At the scale of transects, nest predation rate significantly decreased with increasing shrub cover, given horizontal and herbaceous cover (Table 3). However, this pattern was not observed at the scale of individual nest sites (Table 4). Nevertheless, shrub height was important for explaining nest predation at individual nest sites. Shrub cover and height are thought to be most important in preventing predation by visually hunting predators such as birds (Iones and Hungerford 1972, Picozzi 1975, Autenrieth 1981) rather than mammals that hunt by olfaction (Angelstam 1986, Storaas 1988). However, our data suggest that increasing shrub cover and height may also help reduce mammalian nest predation. Thus, for a given predator density, increased shrub cover and height may reduce Sage Grouse nest predation (Wallestad and Pyrah 1974, Autenrieth 1981, Connelly et al. 1991).

Conclusions

Our results suggest that lower nest predation rates for Sage Grouse may occur in recovering treated sagebrush because the sagebrush treatment reduces the long-term density of predators. This result conflicts with the commonly accepted idea (Lovejoy et al. 1984, Wileove 1985) that habitat fragmentation always increases predation of bird nests. There is little doubt that sagebrush treatment significantly reduces Sage Grouse populations in both the short and long term (Dalke et al. 1963, Braun et al. 1977, Autenrieth 1981). However, the claim that sagebrush treatment increases nest predation rates (Braun et al. 1977, Connelly et al. 1991) is probably not the best reason for preserving contiguous stands

of mature big sagebrush. Treating sagebrush may reduce Sage Grouse populations in the long term for reasons other than nest predation (Braun et al. 1977), including elimination of winter habitat (Homer 1990), removal of year-round thermal cover (Moen 1973, Autenrieth 1981), and reduction of perennial forbs, an important food for hens and chicks (Autenrieth 1981). Consequently, recommendations to preserve mature sagebrush habitats should probably be made on the basis of these factors rather than nest predation.

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